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THE SIGNIFICANT RESULTS OF A DECADE'S STUDY OF THE TUNICATA

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IN any mass of detailed knowledge of organic phenomena, there is sure to be something of general significance for philosophical biology. Under the guidance of this principle I have tried to skim the cream from the results of the last ten years' researches on the Tunicata. These skimmings I present under the following captions:— 1, Taxonomy and Affinities; 2, Distribution; 3, Morphology; 4, Embryology; 5, Physiology.

1. **Taxonomy and Affinities.**— There are several questions of general interest that naturally arise under this head. The Tunicata being a comparatively small class of animals, does the progress made in getting hold of he new kinds indicate that we are approaching completeness in this direction? The class being as thoroughly pelagic at one extreme of its habitat, as thoroughly littoral at another, and as thoroughly abyssal at still another as any class of animals, what is being revealed as to the dependence of number of kinds upon environment? Is the progress of knowledge bringing out anything conclusive as to the greater success of certain types of organization over others because of better adaptation to environment?

Herdman's "Revised Classification of the Tunicata," published in 1891, contains a total of 538 species. This list supposedly includes all the species known at that time. By a reasonably careful enumeration, those described since that year number 521, making a total of 1069 species now known. The better explored portions of the sea, such as the Atlantic about the British Islands, the coasts of Continental Europe, and the Mediterannean, have yielded very few of the new ones, probably not more than half a dozen. The regions that have contributed most are the Australian waters (Herdman and Sluiter); the seas traversed by the Siboga Expedition (Sluiter); the Ceylon region (Herdman); the southern South American region (Michelsen); the Japanese coasts (Oka and Hartmeyer); the Pacific North American region (Ritter);

the west African coast (Sluiter); the Arctic (Hartmeyer); the Antarctic (Sluiter and Herdman); the western tropical Atlantic (Sluiter and Van Name); and the western central Pacific (Sluiter).

As regards the sedentary Tunicata the general statement seems justifiable that *every portion of the sea at moderate depths, when first invaded by the collector, yields a considerable number of new species.* The further conclusion seems warranted that a few more decades of exploration, as active as the last three or four have been, would put us in sight of nearly the whole existing tunicate fauna so far as the open sea and shallower waters are concerned. Experience seems to indicate that here as perhaps in other branches of systematic natural history, after a particular locality has been explored with reasonable care, further collecting does not greatly alter the total number of recognized species. The new ones later brought to light are approximately offset by the elimination of spurious ones from the earlier lists. The slaughter of supposed species of Botryllus by Bancroft should be noted in this connection. Almost certainly the same sort of thing would happen in several other genera, were they to be studied with equal care. This suggestion relative to the rounding out of knowledge of the number of kinds of living tunicates does not touch the question of how in the future it may be found best to classify them.

As to the deployment of the species with respect to the extremes of habitat, of the 521 described since 1892 only about 40 are pelagic. Of these, 10 belong to the Thaliacea, 27 to the Larvacea, and the others to the Pyrosomæ. This is the result in spite of the fact that exploration has been prosecuted little if at all less vigorously in the pelagic than in the littoral realm. This is surely true as regards the Thaliacea and the Pyrosomæ. As to the Larvacea, the minuteness of the animals and difficulty of handling them results in their receiving somewhat less attention than the other groups. There can be no doubt that the living pelagic tunicates are much less abundant in kinds than the sedentary ones. Is this due to the fact that they are subject to less diversity of environment? This explanation is not of necessity the only one. It is possible that the small number of kinds is due to the fact that the group is waning or senescent. I am inclined to think a good case could be made for this hypothesis, at least as regards the Thaliacea. It is by no means impossible that could paleontology give its testimony on the history of this group, as it does for the Cephalopoda and the Foraminifera, for instance it might reveal a richness of ancestral kinds far greater than that presented by the modern fauna.

A matter of prime interest from its bearing on the problem of fitness to survive is the large number of kinds (species?) belonging to a few of the genera, or sets of illy separated genera, of sedentary ascidians. The most conspicuous groups from this standpoint are 1 Ascidia; 2, Molgula; 3, Cynthia with its close ally Rhabdocynthia; 4, Styela with the scarcely distinguishable Polycarpa; 5, Botryllus and its close congener Botrylloides; 6, Amaroucium with its near relative Aplidium; and 7, Leptoclinum. These seven groups contain more than 600 of the approximately 1000 species of simple and compound ascidians now described. There are recognized at least 80 genera in these two tunicate sections. In other words, as our scheme of classification now stands less than 14% of the genera contain fully 60% of all the species. It will be observed that these few prolific groups present all the leading types of sedentary ascidian organization. An analysis of the species in these groups with reference to the character of their environments would certainly not show that some of the types tend to be restricted to one set of external conditions while others are restricted to different conditions. *I do not believe there is anything in our present knowledge of ascidian structure, function, or distribution, to warrant the conclusion that the groups most abundant in kinds are so because of their greater fitness to survive, or their relative adaptability to external conditions.*

Little headway has been made toward determining the extrinsic affinities of tunicates. Indeed although nothing has turned up to shake confidence in their chordate nature, some of the newer results are puzzling rather than enlightening. Thus Goldschmidt reports the embryology of Appendicularia (strictly Oikopleura) to be so similar to that of the typical ascidian that little hope can be entertained of further light on the problem from this direction. He confirms the contention of Seeliger and others that there is no real metamerism in the tail of this animal. I have examined a number of stages in the larval life of a species of Oikopleura and am able so far to testify to the correctness of Goldschmidt's observations. On the other hand Metcalf finds some evidence of metamerism in the rapheal nerve of the Molgulidæ. Perhaps these facts slightly support Perrier's view that the adult sedentary simple ascidian is nearest to the vertebrate ancestor and that consequently Appendicularia is a modified ascidian larva.

Seeliger and Metcalf doubt that there is a true homology between the tunicate and vertebrate hypophysis. Neither does Seeliger believe the vertebrate thyroid to be related genetically to the tunicate endostyle.

Largely from the character of the stigmata and the absence of an epicardium, Julin holds a Mediterannean species called by him *Archiascidia* to be the most primitive ascidian.

As to intra-class kinships, perhaps nothing of greater general interest has come to light during the decade than that Octacnemus is an ascidian proper and has nothing to do with the Salpidæ. Metcalf and Ritter have made this positive.

The polyphyletic character of the compound ascidians is now admitted by probably all students of the class.

2. **Distribution.**— Some of the most interesting questions under this head are presented by the abyssal fauna. We now know at least 25 species that belong here and about half of these come from depths of 2000 fathoms, more or less. Some of the genera represented in this deep-sea fauna, though widely separated systematically, still present a common trait in the tendency to retrogression of the branchial apparatus. This is distinctly seen in genera so far asunder as Culeolus, Octacnemus, and Hypobythius. On the other hand species of familiar littoral genera are coming up from time to time from great depths, having no marks whatever that can be regarded as impressed upon them by their peculiar environment. For example I have now in manuscript the description of a Styela from 2200 fathoms off the California coast, which does not differ from several shore species more than these latter differ from one another; neither do its specific marks betray anything of the peculiarities of its habitat. No aspect of observational as contrasted with experimental natural history promises more light on the nature of species, so it seems to me, than do faunas of the profound ocean depths.

The cosmopolitanism of some of the pelagic species, notably *Salpa runcinata fusiformis*, is significant. It appears as if there is no part of any sea in which this animal does not flourish. Perhaps the data yet in hand do not warrant quite so sweeping a statement, but it is borne out by material now in my possession from many parts of the Pacific, and by already published data from other oceans. This Salpa is a close rival of some species of Sagitta and of *Eucalanus finmarkicus* in this regard.

We now have sufficient information about Arctic ascidians (Bonnevie, Kiear, Huitfeldt-Kas, Hartmeyer), and about those of the Antarctic (Herdman, Sluiter), to make it clear that this group lends little support to the "bipolar" theory of distribution. Fifteen years ago Herdman concluded that sedentary tunicates are more numerous in species, and are in general of larger size in higher latitudes than in the tropics and subtropics. In spite of some rather rich collections recently described from tropical waters, notably from Bermuda and the East Indies, it seems as though the generalization will stand. My own somewhat extensive experience with Pacific Ocean ascidian faunas appears to support it.

3. **Morphology**.— Knowledge of the adult anatomy of the group has been enriched in many directions. The structure of the appendicularian "haus" has revealed, particularly through the patient labors of Lohmann, an elaborateness that puts it along side the sting of the honey-bee as a puzzle to the student of adaptations. For one thing the apparatus turns out to be a strainer of the most exquisite fineness.

One of the most interesting results of Salensky's extensive studies on the anatomy of appendicularians is that the heart of these animals is far more simple than was supposed, and that it is probably homologous with the procardial organ of the ascidian proper.

Branching of the nuclei of some of the ectodermal secretory cells of Oikopleura occurs to such an extent that it may well attract the attention of those interested in general problems of cell structure and activity.

Metcalf's findings relative to the fusion or intergradation of nervous and glandular tissues in the neuro-glandular complex of several ascidians is noteworthy. Of general significance also may be mentioned the tendency to multiplication of ganglionic outgrowths observed by Metcalf in Salpa.

4. **Embryology.**— Knowledge of tunicate development has progressed in numerous ways during the decade. According to my judgment two of these are particularly significant to the general biologist. They pertain to the very early embryonic life and to the multiplication of branchial stigmata. Among the investigations of the early embryo those by Conklin easily hold first place. To the embryologist, one set of facts brought out by Conklin stands with special prominence in the midst of many that are important. These relate to the question of organization in the unsegmented egg. Conklin's figures seem to furnish strong support for his statement that "it is doubtful whether any other case of cytoplasmic localization hitherto reported is more remarkable than that which has been described in the preceding pages for the ascidian egg."

Important as are these particular truths of ascidian development emphasized by Conklin's observations, there are other aspects of his work which appeal particularly to the general zoologist. In a résumé of what is known about cytoplasmic localization the author says:— "The annelids do not approach the chordates nor the echinoderms in the earliest stages of localization any more closely than in their cleavage stages or later development. *In short there is no convergence toward a common type of localization as one goes back to earlier and earlier stages in the ontogeny.*" In another connection Conklin points out that the pigmentation of the ovum which has served him so admirably in making out the "specification" in the development of Cynthia "may differ most remarkably in different genera of ascidians"; and that "the same may also be said of the yolk." Of the pigment he says, "this inert substance is not in itself of differential value, but it lies in a definite region of the egg and probably in a particular kind of protoplasm." The general zoologist, particularly the taxonomist, must inquire in the presence of these facts, Where is this sort of discovery going to lead us? If, viewing developing animals broadly, we find types of presegmental localization or in ordinary terms, types of *egg structure* that do not converge to a common type; and if eggs from genera so closely related as Cynthia[1] and Molgula differ remarkably in "kinds of protoplasm," does it mean that by and by we are going to find specific characters in the eggs of aminals as well as in their adult condition? For my own part, speaking as a systematist, I am fully prepared to accept the full consequences of just this outcome. Furthermore I see something of the reach of such consequences.

The fact about the development of branchial stigmata which seems to me second in significance only to cytoplasmic localization, is that the origin of the epithelium of new stigmata is always dependent on that of preceding ones. The general question of how repetitive parts arise is basal. These results on the branchial stigmata of ascidians seem to be decisive so far. Selys-Longchamps, Dumas and Julin are specially to be mentioned in these investigations.

The somewhat bizarre notions which gained currency some time ago about the origin and fate of the follicle cells of the ascidian ovum seem to have been pretty nearly disposed of during the decade, thanks to Floderus, Bancroft, Todaro, and Korotneff.

Origin of the heart from the ectoderm is affirmed by Salensky. He treats this along with other instances of ontogenic origin of ascidian parts in defiance of rigid germ layer tenets, under the term "heteroblasty." This general subject, important as it is, has received no thorough investigation during the decade.

The regular succession of generations of ascidiozoids in the Botryllus colony observed by Pizon and Bancroft is a significant enlargement of our knowledge of development on the plane of organic animal societies.

5. **Physiology.**— Studies of the degeneration and rejuvenation of colonies of compound ascidians (Pizon, Caullery, Bancroft) have yielded significant results. For one thing the dying down of the colonies seems to be at least partly a normal senescent phenomenon and not due to the direct influence of environment.

Colonial as contrasted with zooidal individuality is suggested particularly by studies on growth and blood circulation in the Botryllus colony. The interesting fact is brought out by Bancroft that the ectodermal ampullæ in the test substance of the Botryllus colony are rhythmically contractile and have a regular circulatory office. There is coordinated activity among large numbers of ampullæ in the same colony and this seems to be without the intermediation of the nervous system.

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[1] Attention should be called to the fact that if Conklin's eggs were from the *Halocynthia partita* of Verrill, he was really dealing with a Styela and not with the genus Cynthia at all.

The unique form of tunicate heart action has continued to attract attention. The most comprehensive study of it is by L. Schultze on Salpa. "The heart of Salpa is an example of purely muscular self-regulation in a highly coordinated mechanism of motion." This sentence summarizes Schultze's positive results. Neither cerebral influence nor blood pressure play a causal part in the phenomena. Of similar general import Bancroft and Esterly find proof of polarization through its own activity in the heart of Ciona. On the other hand Magnus, Hunter and Fröhlich bring forward rather strong evidence of the dependence of heart action in Ciona on ganglia and to some extent on the brain.

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